each tarsus, besides a few others. The penis is placed on the ventral surface in the median line between the hinder part of the coxæ of the third legs; the vulva between those of the second legs.

I found the creature on the surface of, or very slightly buried in, a depression of the skin lining the inner side of the external ear of the short-tailed field-vole (*Arvicola agrestis*). I believe it to be unrecorded, and propose to call it "*Goniomerus musculinus*."

DESCRIPTION OF PLATE XXVI.

Fig. 1. *Myocoptes tenax*, ♀. Dorsal aspect. × 175. Drawn from a specimen with long abdomen.
2. „ „ „ Ventral aspect. × 175. Drawn from a specimen with short abdomen.
3. „ „ „ From the side. × 175. Natural position, holding the hairs of the mouse.
4. „ „ ♂. Dorsal aspect. × 175.
5. „ „ „ Ventral aspect. × 175.
6. „ „ nymph. Dorsal aspect.
7. „ „ ♀. 3rd leg, seen from the inner side. × 350.
8. *Symbiotes tripilis*, ♀. Ventral aspect. × 130.
9. *Goniomerus musculinus*, ♂. Dorsal aspect. × 175. (There is another pair of long hairs on the hind margin, below and hidden by the pair shown.)

On the Structure of the Retina of the Blowfly (*Calliphora erythrocephala*).

By Benjamin Thompson Lowne, F.R.C.S., F.L.S., Hunterian Professor of Comparative Anatomy in the Royal College of Surgeons.

[Read 21st February, 1889.]

(Plate XXVII.)

In 1884 I had the honour of reading a paper before this Society on the compound vision and morphology of the eye in insects, which was published in the second volume of the new series of 'Transactions.'

That paper received at the time much adverse criticism, and Dr. Hickson published a memoir in the 'Quarterly Journal of Microscopical Science,' in which he convinced himself that he had completely refuted my observations.

From that day to this I have continued to work at the subject, and I now venture to bring before this Society evidence which I think can hardly fail to convince even the most sceptical of my opponents. Although I never had any doubt of the correctness of my figures or descriptions, I felt it incumbent upon me to produce preparations which would admit of no double interpretation, but which would appeal at once to the eyes of those who are only partially acquainted with the histology of the vertebrate retina.

At the time I published my former paper I felt so certain that the views I held would receive a ready acceptance, that I did not, perhaps, enter sufficiently into minute details, and left many points to be investigated by other workers. I have since examined every structure in the greatest detail, and have much to add with regard to the developmental history of the compound eye.

The retinal rods, which I figured correctly in my former paper, correspond with the periopticon of Dr. Hickson, except that his figures show that every vestige of nerve-structure and nerve-terminal organs had been completely destroyed in his preparations, leaving nothing but the skeletal framework with the tracheal vessels, which he has delineated most carefully and correctly.

He states that my paper and investigations were unnecessary, owing to the unanimity of previous investigators: none, however, agree in any detail with Dr. Hickson, nor, so far as I am able to judge, to any considerable extent with each other.

Putting aside for the moment the earlier observers, the so-called periopticon of Hickson has only been described in detail by Berger, Carrière, Ciaccio, Viallanes, Hickson, and myself.

To show how far these observers agree with each other and with the older writers, I will quote a few sentences from Dr. Hickson's paper. He says:—

"Previous to the publication of Berger's paper the optic tract of insects had been briefly described and names given to the various regions. Thus Weismann called the opticon and epiopticon the 'bulbus,' the region where the optic fibrils decussate the 'Stiel,' and the periopticon the 'Augenscheibe'" (*l. c.* page 27).

Even the most cursory acquaintance with the work of the German naturalist would have shown Dr. Hickson that this is an egregious misstatement of Dr. Weismann's nomenclature.

Weismann's 'Stiel' was the optic nerve, and his 'Augenscheibe' the structure from which the dioptron is developed. I shall have later to give Dr. Weismann's views more fully. Dr. Hickson continues (page 27):—"Since Berger's paper appeared Carrière has described the periopticon as 'a layer of long palisade-shaped cells, the number of which corresponds with the eye units; every one of these palisade cells possesses an oblong nucleus at its foremost, somewhat broader, end.' My researches show that this description is quite inaccurate. The elements of the periopticon are not cells, and the large oval nucleus situated in each element does not exist; nerve-cells, when they exist in the region of the periopticon in *Musca*, lie between the elements and not in them, as my figures show."

These statements and others show that Dr. Hickson and Carrière do not agree. With regard to the nuclei described by Carrière, they undoubtedly exist, but not, as Carrière thought, within the palisades, but externally to them, immediately beneath their investing sheath. Dr. Hickson is right when he says these bodies are not cells, they are developed from cells, and each consists of a bundle of fusiform rods. With regard to the terminations of the optic nerve, Carrière distinctly traced the nerve-fibres into the palisades; Dr. Hickson says they go round them. I trace them directly into the fusiform rods which form the palisades. The structures seen and correctly figured by Dr. Hickson are tracheal vessels.

Carrière supposed the nerve-fibres to pass out at the superficial end of the palisades and to perforate the basilar membrane; from this I entirely dissent. In support of this view Carrière has figured, quite diagrammatically, what I believe is a tracheal vessel seen behind the fusiform body. Carrière also saw the highly refractive outer ends of the rods, or, rather, that part which is connected with their inner portion, and says, "in *Musca vomitoria* one sees in every cell a cylindrical axis."

Dr. Hickson entirely put himself in the wrong in describing the nervous elements as between the palisades; his nervous elements are undoubtedly fine tracheal tubes. Dr. Hickson's figures accurately represent the nerve-sheaths and tracheæ as well as the supporting neuroglia, but no vestige of nerve or nerve-end organs appears in them. A careful examination of his own figures at once leads to a dissent from all his statements, which are as inaccurate as his figures are accurate. I cannot understand how so good an observer could have been so misled.

Berger and Viallanes trace the optic-nerve fibres through a series of small round cells, very conspicuous in the outer half of my retina, Hickson's periopticon. Hickson regards these cells as of quite secondary import. They clearly belong to the supporting tissue and are external to the sheaths of the retinal elements, which are continuous with the perineurium of the optic nerve.

Dr. Hickson and Dr. Grenacher suppose the sheathing cells of the great rods, retinulæ of Grenacher, to be the nerve-terminals; and more recently Platten pretends that the optic nerve terminates in the crystalline cone. There is therefore no unanimity amongst previous writers, especially in matters of detail; as it is impossible that they can all be right, it is quite possible, as I assert, that they are all wrong.

Dr. Hickson's neurospongium, or terminal anastomosis, which is inadmissible on physiological grounds, is no nerve-plexus at all, but the tracheal plexus and the sustentacular framework of my retina.

It is exceedingly difficult to prepare sections which show the true retinal end-organs. This difficulty arises from the fact that the chloroform and alcohol used in the process of imbedding dissolve the fatty matters from the nerves, and the external extremities of my retinal rods are completely dissolved or disintegrated by the action of aqueous media.

I have, however, on many occasions succeeded in obtaining sections in which both the inner and outer extremities of the retinal rods, as well as the nerves, remain more or less unaltered. Another difficulty arises from the extreme transparency of these structures in very thin sections, and from the fact that they cannot be stained by any of the stains used in such researches; the outer ends of the rods are not affected by strong solutions of aniline dyes, except vesuvin *.

In thicker sections the numerous round cells between the retinal nerve-end organs, which are not connected with nerves, but with the sustentacular framework, entirely conceal the outer ends of the rods.

There are two methods which give good results; in both the tissues must be fixed either with osmic acid and absolute alcohol

* The best demonstration of these organs is obtained by staining with a solution of vesuvin in aniline water. The solution must be quite freshly made, and unfortunately such preparations fade rapidly when mounted in balsam.

or in absolute alcohol, and imbedded in paraffin without the use of ether or turpentine. Very thin sections are then cut and fixed on the slide with shellac and kreosote. The cement must be thoroughly dried in the oven at the melting-point of the paraffin used, and on no account at a higher temperature.

The paraffin is next removed by turpentine. The slide is then wiped on its back and edges, and flooded with pure spirit, which is drained off, and immediately afterwards flooded with 75 per cent. alcohol and rapidly drained; Erhlich's logwood solution is then poured on the slide and washed off after a few minutes or longer by agitating the slide for a few moments in water, and it is again flooded with 75 per cent. alcohol. The washing is the most dangerous process, as if the specimens are kept too long in water the outer ends of the retinal rods will be entirely dissolved. Instead of Erhlich's logwood a solution of vesuvin in water may be used; it stains the retinal-end organs better than any of the aniline dyes. Saffranine in 50 per cent. alcohol, or a solution of fuchsine or eosine, may be used for staining, and the washings done with spirit, the results of which are often satisfactory. Spiller's purple gives excellent results, but the specimens are not permanent. The specimen, after flooding with 75 per cent. alcohol, is treated with pure alcohol, rapidly drained and cleared with clove-oil and mounted in balsam.

Or, after the first washing in water, the specimen may be mounted in glycerine, gradually adding stronger and stronger glycerine and water, and draining after each addition. I have found that with aniline dyes a very dilute solution of sodium carbonate, ·5 per cent., or aniline water is not inadmissible for washing out the excess of the stain.

Glycerine mounts, when successful, show the outer ends of the rods, either vacuolated or frequently partially dissolved, more plainly than balsam mounts.

The balsam mounts need very careful illumination, otherwise it is impossible to see the outer ends of the rods.

If we trace the optic nerve, we observe that its fibres run in larger or smaller bundles, invested in a very transparent sheath, or perineurium. They terminate in the palisade layer by entering the fusiform elements. The sheath is continued over the fusiform elements, and terminates on the inner surface of the basilar membrane. The tracheal vessels accompany the bundles of optic nerve-fibres, outside their sheath, and continue between the pali-

sades, and ultimately pierce the basilar membrane and run between the great rods.

The figure given (Plate XXVII. fig. 1) is from the eye of a Hawk-moth, in which these details are larger and more easily seen than in the Blowfly. The palisade bodies do not reach the basilar membrane, but are prolonged as extremely transparent rods, 3 to 5 μ in diameter, in the fly and in most of the insects I have examined, and from 20 to 30 μ in length (Plate XXVII. figs. 2 and 3, *a*). These with the palisade cells, *b*, form my bacilli or retinal end-organs, the whole length of which is from 60 to 70 μ. The outer transparent portion is rarely straight, but usually strongly curved in a crook. They exhibit a fine longitudinal striation.

The outer ends of the rods evidently consist of some substance resembling mucin; they have the same refractive index and general characters as the mucin of the intestinal epithelial cells of the insect.

The inner extremity of the outer part of the rod is imbedded in the fasciculus of elongate cell-like palisade bodies, fig. 2, which form the inner portion of the retinal end-organs; each outer segment appears to be made up of a number of finer rods, 2 μ in diameter, pressed together into a cylinder; these produce the longitudinal striæ. Each small component rod lies on the inner surface of one of the fusiform cell-like bodies which form together the inner part of the retinal end-organ.

The outer ends of the rods are surrounded and, except in very thin sections, concealed by the small round chaplet-cells of Viallanes (fig. 2, *c*). These are connected with each other by fine processes and form a true adenoid sustentacular tissue, well seen in transverse sections of the pupa (fig. 4).

Comparison of the Bacillary Layer with the Bacillary Layer of the Vertebrate Retina.

In size and structure the elements of the retina are almost identical with those of the vertebrate; the optic nerve terminates in the protoplasmic inner segment, whilst the outer segment is transparent, resists stains, exhibits longitudinal striæ, and swells up with water in both. In both it is easily destroyed, and frequently exhibits vacuolation.

In most insects the outer, highly refractive ends of the retinal end-organs are imbedded in abundant pigment. The flies are the only exception, and in these the cells surrounding the bacilli are free from pigment.

The Tracheæ (Plate XXVII. fig. 3) form a dense network around the inner segments of the retinal end-organs in insects, and branches extend to and perforate the basilar membrane. These fine tracheæ are without any spiral markings, and are easily mistaken for fine nerve-twigs. The figure given (fig. 3) shows these tracheæ in a moth, and it can be readily seen that they lie between the nerve-end organs, and that they branch dichotomously between the great rods. The aniline stains at once colour the tracheæ, whilst they have no effect upon the nerves. These stains, however, attack the nerve-sheaths, but not the outer ends of the retinal end-organs. By the use of aniline stains, especially Spiller's purple, I have been able to trace the finer tracheal vessels, which have been constantly mistaken for nerves, to the larger tracheal trunks and in one of my photographs this relation is sufficiently evident.

The illustrations on Plate XXVII. show the large size of the bundles of optic nerve-fibres with their terminations in the retinal end-organs; they also show that nothing bearing any proportion to the magnitude of these nerve-cords passes through or even up to the basilar membrane. The basilar membrane is chitinous and has a cellular layer on both its inner and outer surface; that on its inner surface consists of branching or stellate cells, which are continuous with the sustentacular framework of my retina; the outer layer consists of pigment-cells, continuous with the pigment-sheaths of the great rods. The perforations in the chitinous layer of the basilar membrane are between and not opposite to the extremities of the great rods, and transmit the tracheal vessels.

The structure of the great rods has with some been the difficulty in accepting my views. The appearance of these structures in many sections is certainly perplexing. The reason is that which I have already insisted upon. In life they are hollow tubes filled and distended with fluid. In bad preparations they appear stellate in transverse sections and present no central cavity; in radial sections they are separated from each other by wide spaces, often filled by distended tracheal vessels.

In transverse sections, when unaltered by the process of imbedding, they are circular or hexagonal rings, with a large central cavity; they touch each other at their periphery, and the tracheal vessels appear as thick-walled but very small tubes. Each great rod is seen in such sections to be lined by a thin cuticular layer, which dips down between the sheathing cells; it is the folds of this membrane which appear as bright highly refracting points under unfavorable conditions of illumination. With direct central light, thin sections, with oil or water immersion-lenses, no longer present these appearances; there is no bundle of axial rods in such preparations when properly examined, only a thin cuticular lining.

Further evidence in favour of my views is, I believe, shortly forthcoming from the pen of an independent observer. Prof. Plateau informs me that last year, at Cologne, Dr. Exner showed the single image formed by the compound eye—the image in the plane of my basilar membrane formed by the uninjured eye, *i. e.* by my dioptron. I wait anxiously for the spring, as with fresh insects at command I have little doubt the demonstration of an erect picture in this region is perfectly easy.

The Development of the Compound Eye.

The development of the compound eye was described by Weismann in 1864 *. I have gone through a most laborious research, and in the main points my observations agree with those of the great German investigator. Weismann says it has long been known that the eye in insects is developed from two perfectly distinct parts—one from the nerve-centres of the larva, the other from the optic disc ("Augenscheibe," *l. c.* p. 194).

If we follow the development of the optic disc, we find it at first as a thin cellular expansion enveloping the anterior part of the hemisphere (or supra-œsophageal ganglion). It consists of cells (the optogenic cells of Viallanes) which are larger than those of the other discs; they measure 15 μ in diameter at an early period of the pupa state and have large clear nuclei. During the formation of the head, the eye-disc separates considerably

* "Die Entwicklung der Dipteren," Leipzig, 1864. Reprinted from Köll. Zeitsch. f. w. Zool.

from the hemisphere, the interspace being filled with the granular yelk-like substance of the somatic cavity of the pupa. The whole dioptron is developed by a division of the optogenic cells, as Claparède long ago showed. Each original cell corresponds to a single corneal facet. These cells form almost hemispherical projections on the outer surface of the disc and are soon covered by an extremely thin cuticular layer.

The cuticular layer is seen in my sections to dip slightly between the cells, whilst the corneal lens is secreted subsequently between the cell and the primitive cuticular layer. The lenses are, as I have already described them, perfectly distinct from the chitinous layer, giving rise to the condition I have designated the kistoid cornea. In adult pupæ the distinction is perfectly apparent, although Dr. Hickson has denied that my description is correct; the most patient reinvestigation entirely confirms my former statement.

So far my investigations entirely accord with Weismann's description. Weismann, however, believes that the great rods contain a nervous structure, which he describes, from optical sections, as resembling a bundle of fine, highly refractive, conducting threads ending at the crystalline cone. He has nothing to say of their manner of development, and only expresses the opinion that they appear more like definite threads than the angles of a solid rod.

These so-called axial threads, as I have stated above, are well seen in numerous transverse sections to be mere folds of a chitinous membrane enclosing a considerable empty cavity.

Weismann's description of the development of the nervous structures is as follows:—"The thin nerve-cord (*Stiel*) which unites the optic disc to the hemisphere still appears on the fifth day as a nervous cord; but on the twelfth day the pedicle can no longer be seen." He concludes, however, that it has spread out into an invisible layer over the whole surface of the ganglion. That he should have arrived at such a conclusion without sufficient evidence is quite unlike him. If, as he says and as is certainly the case, the nerve disappears entirely between the fifth and twelfth day, the opinion that the radial striæ (which, he says, appear later between the disc and the hemisphere) are the same nerve spread out, is not founded on fact.

We must remember that Weismann regarded the discs as

expansions consisting of epiblast-cells. It was Ganin who, ten years later, first made sections and discovered their real structure. He found three distinct layers—Weismann's epiblastic layer; his own provisional layer, which covers it externally as a fine cellular expansion, which resembles the amnion of a mammalian embryo in being continuous with the periphery of the disc, in covering its whole outer surface, and in enclosing a cavity between it and the epiblast of the disc; and the mesoblastic layer, which fills the hollow cup-like cavity on the inner surface of the epiblastic layer, and which consists of a network of fine branching cells.

Weismann's own figure (52, plate xiii., *l. c.*) shows clearly that his supposed optic nerve is the mesoblast of the disc. My own observations show that the nervous pedicle of the optic disc becomes atrophied and disappears, whilst the nervous retina is developed as a papilla in front of the original optic pedicle.

In my former paper I described and gave figures of the manner in which a new retina is developed during the skin-shedding of the Cockroach; the original nervous pedicle of the disc corresponds to the nerve of the first few facets of the eye. As the number of facets is far greater after each ecdysis, so a new retina is developed from the nerve-centres as a distinct papilla; the first formed nerve and retina at the same time undergo atrophy.

I regard the original pedicle of the disc in the Blowfly (figs. 5, 6, & 7, *st.*) as a rudiment. It exhibits few, if any, nerve-fibres and consists chiefly of connective neuroglia continuous with the investing layer of the rudimentary hemisphere. The spongy mesoblastic tissue which Weismann mistook for an expansion of the nervous pedicle of the disc consists of the elements from which the tracheal vessels and pigmented fringes of the dioptron and neuron originate. This tissue extends into the dioptron, but only between the ingrowing optogenic cells, which become first columnar and then elongated rods, dividing during the process to form the cone and the investing cells of the great rods, and separating from each other to enclose the central cavity of the cone and the great rod. Claparède long ago correctly described the manner of the development of the cones and great rods.

Viallanes, like Weismann, but with less excuse, mistook the mesoblast of the disc for the optic nerve and believed that its fibres perforate the axes of the great rods. It is easy in thick

sections to mistake fibres running between for fibres entering the optogenic cells.

The nerve-papilla, from which the optic ganglia, the optic nerve, and the retina are developed, gradually grows outwards towards the dioptron (Plate XXVII. figs. 5–8, *n*). It is at first covered by a layer of columnar cells, which represent the epiblast of the nerve-centre; from this layer the bacillary layer of the retina is developed. These cells become converted into the retinal end-organs. The mesoblastic spongy tissue is gradually absorbed or converted into tracheal and connective elements, which ultimately form a thin layer between the retina and the basilar membrane of the dioptron.

The retina, even when the insect is nearly ready to escape from the pupa, is still separated from the dioptron by a space filled with branching cells (Plate XXVII. fig. 8, *mc*) and secondary yelk, so that the supposed entrance of nerve-fibres into the dioptron cannot be explained by any known process of development.

The continuity of the tracheæ of the dioptron and those of the mesoblast is the result of the penetration of the latter between the great rods during their inward growth; but during this period the nervous papilla is separated by a wide space filled with secondary yelk and reticular mesoblast from the ingrowing epithelial structures of the dioptron.

Thus, if my observations are correct, the retina, like that of a vertebrate, is entirely formed as an outgrowth from the central nervous system, while the dioptron, like the crystalline lens and the refractive structures generally, is formed from the external epiblast, which is more or less invaded by mesoblastic elements. With regard to the retina itself, it is undoubtedly, like the nerve-centres, no less epiblastic in the insect than in the vertebrate, as the hemispheres themselves, as well as the ventral ganglia, are formed from the embryonic epiblast.

In conclusion, I would add that it is scarcely fair to expect me to prove a negative, *i. e.* that no nerve-fibres pass to the dioptron. The onus rather lies with my opponents to prove that the great optic nerve does enter the dioptron, and to find its terminals. Even the most cursory glance at the works of Dr. Hickson, M. Berger, M. Viallanes, and others will show that they have given totally dissimilar representations; of these Dr. Hickson's are correct enough as representations of tracheal and mesoblastic skeletal tissues. I would ask, Which of the various structures

represented are to be considered as nerves? No one has yet figured one satisfactory representation of the optic-nerve fibres entering the great rods. Dr. Hickson says, "Morphology teaches us that the great rods are nerve-terminals." To appeal to morphology to settle the question appears to me to show on how slender a basis of observation the received view rests, and I should myself regard an appeal to morphology as one which is fatal to the received view; for, if morphology teaches us anything on this subject, it is that the retinal end-organs belong to that part of the epiblast from which the great nerve-centres are developed, and that the dioptric structures arise from the superficial or cutaneous epiblast.

DESCRIPTION OF PLATE XXVII.

Fig. 1. A section of the retina of a Hawk-moth; partly drawn from a photograph and finished from the section. *gt*, great rods; *m*, basilar membrane; *b*, bacillary layer; *n*, optic nerve; *tr*, tracheal vessel.

2. A section of the retina of a Blowfly. *c*, chaplet-cells of Viallanes. $\frac{1}{12}$-inch objective, water-immersion.

3. A portion of the retina of a Hawk-moth; drawn from a photograph, with details added from the specimen. The tracheal vessels seen passing through the basilar membrane are much more distinct in the photograph than in the specimen seen by the microscope; these are represented in the drawing as they appear in the photograph.

4. A transverse section through the bacillary layer of the retina of a Blowfly which had just emerged from the pupa.

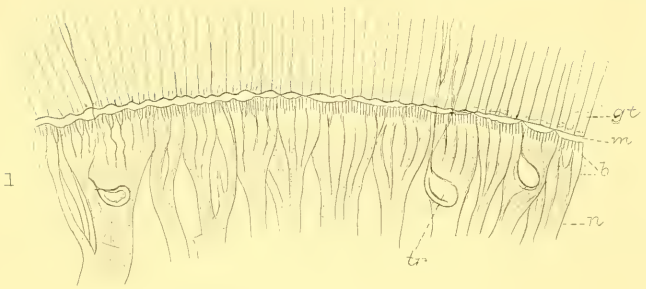
5. A section of the optic disc and cephalic ganglion of a 3-day-old pupa. *o*, optic disc; *st*, stalk; *rt*, retina. 1-inch objective.

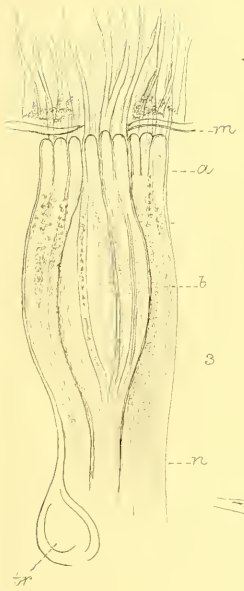
6. A portion of the same, showing the retina and inner extremity of the stalk.

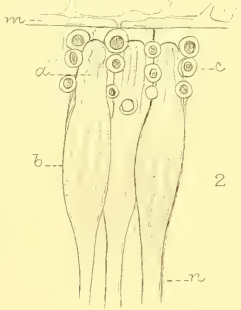
7. A portion of the optic disc and stalk of the same. *oc*, optogenic cells; *mc*, mesoblastic cells. $\frac{1}{4}$-inch objective.

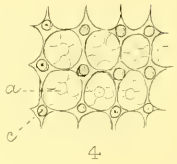
8. A section of the retina of a ten-day-old pupa. Showing the mesoblast elements between the retina and the basilar membrane. $\frac{1}{4}$-inch objective.

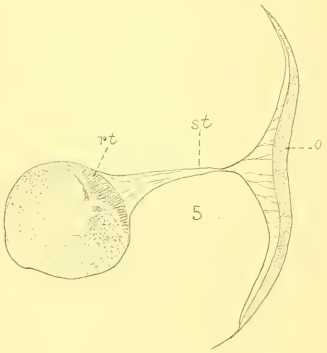
(The letters indicate the same parts in all the figures.)

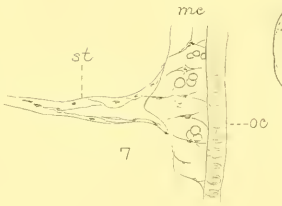


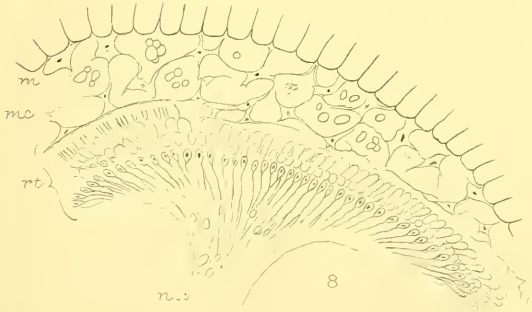


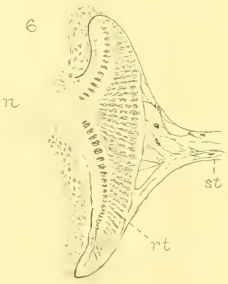












B.T.L. del. ad nat. Bemrose & Highley lith. West, Newman imp.

RETINA OF BLOWFLY.